

An Analysis of Host Range in the *Diadegma nanus* group of Parasitoids in Western Europe, with a Key to Species (Hymenoptera: Ichneumonidae: Campopleginae)

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Abstract.—From a base of 768 rearings from microlepidoptera, host range characteristics are recorded and analysed for 24 Western Palaearctic species of *Diadegma* (Ichneumonidae: Campopleginae) that may represent one or more natural groups. Some speculations on the evolutionary ecology of host range and speciation are made. A key to these species, and a further six that have not been reared, is provided. *D. germanicum* Horstmann 1973 is synonymised with *D. longicaudatum* Horstmann 1969, and *D. consumptor alpestrator* Aubert 1971 with *D. consumptor consumptor* (Gravenhorst 1829).

The genus *Diadegma* Förster (Ichneumonidae: Campopleginae) is a very large genus of koinobiont endoparasitoids of Lepidoptera, attacking the host in its larval stage and killing it in its cocoon. *Diadegma* has a worldwide distribution, and an overall host range centred on smallish moths in the “lower ditrysian” superfamilies (sensu Scoble 1992), forming a large part of the traditional “microlepidoptera”. Several species are important natural enemies of pest Lepidoptera.

The purpose of this paper is to examine the host ranges of Western Palaearctic species in a defined part of the genus *Diadegma* (the *nanus* group) and to provide a key to the included species. We also summarise the known distribution of each species, and make some taxonomic remarks. It has been pointed out by Fitton & Walker (1992), writing on several economically important *Diadegma* species, that hitherto there have been neither careful taxonomic revisions within *Diadegma* nor sufficiently critical assessments of species-level host range, with the consequence that the body of literature on given species is of very limited worth.

A considerable quantity of reared material of the *Diadegma nanus* group has been obtained, most of it recently, and carefully evaluated. Although 63% of this material is in the National Museums of Scotland, we have made efforts to source all available material. As well as trying to understand and express the host ranges of particular species from fairly rich quantitative data (altogether 768 rearings) there is the opportunity to try to analyse the patterns seen between species from the perspective of evolutionary ecology. In particular, from evidence seen in a braconid genus *Aleiodes* (Rogadinae), it has been hypothesised (Shaw 1994) that there is a tendency in some koinobionts to broaden their host ranges, and that this can precede the birth of new species as extreme specialists. While we will argue that a formal test of the hypothesis remains out of reach, the *Diadegma* data can certainly be used to revisit some of its general predictions.

The *Diadegma nanus* group of the subgenus *Nythobia* Förster, as defined here, includes the species groups I and II in

Horstmann (1969: 421 ff.), but without the species that subsequently have been transferred to the genera *Campoplex* Gravenhorst (*maculifemur* (Strobl), syn. *anthracostoma* (Strobl)), *Enytus* Cameron (*apostatus* (Gravenhorst), *neopostatus* (Horstmann), *parvicanda* (Thomson)), *Eriborus* Förster (*dorsalis* (Gravenhorst)), *Lathrostizus* Förster (*monilicornis* (Thomson)) and *Tranosemella* Horstmann (*praerogator* (Linnaeus), syn. *interrupta* (Holmgren), syn. *lacticrus* (Thomson)) or to the subgenus *Diadegma* Förster s. str. (see Horstmann 1969: 429 ff.). It is characterized within the genus *Diadegma* Förster s. l. by the hind tibiae being whitish or yellow basally and usually having a darker ring or patch subbasally, and in the female sex by the caudal edge of the sixth and seventh tergites of the gaster being not or only very slightly incised dorsally.

No claim can be made that the *nanus* group overall is monophyletic. However, four subgroups might be distinguished and, although the differences between them are poorly characterised, there is a better prospect that further research could show these to be monophyletic:

1. *Diadegma nanus* subgroup: Ovipositor sheaths 0.3–1.5 times as long as the first tergite of the gaster, ovipositor weakly upcurved. Claws inconspicuously pectinate (as in Fig. 7), the subapical teeth less than half as long as the apical one. The foregoing characters are probably symplesiomorphies, but possible synapomorphies are small size coupled with parasitism principally of leaf mining microlepidoptera. Species: *anurum* (Thomson), *brevivalve* (Thomson), *callisto* Horstmann, *crassum* (Bridgman), *crataegi* Horstmann, *duplicatum* Horstmann, *elishae* (Bridgman), *exareolator* Aubert, *holopygum* (Thomson), *laricinellum* (Strobl), *lithocolletis* Horstmann, *melanium* (Thomson), *micrurum* (Thomson), *nanus* (Gravenhorst), *pusio* (Holmgren), *rufatum* (Bridgman), *scotiae*

(Bridgman), *stigmatellae* Horstmann, *tamariscator* Aubert.

2. *Diadegma latungulum* subgroup: Ovipositor sheaths 1.4–1.6 times as long as the first tergite of the gaster, ovipositor straight (as in Fig. 15). Claws conspicuously pectinate (possible autapomorphy), the subapical teeth nearly as long as the apical one (Fig. 6). Parasitoids of *Mompha* species (Momphidae). One species: *latungulum* (Thomson).

3. *Diadegma consumptor* subgroup: Ovipositor sheaths 1.1–2.0 times as long as the first tergite of the gaster, ovipositor straight (possible synapomorphy) (Fig. 15). Claws inconspicuously pectinate (Fig. 7), the subapical teeth less than half as long as the apical one. Parasitoids of Psychidae (as far as known: possible synapomorphy). Species: *consumptor* (Gravenhorst), *ledicola* Horstmann, *longicaudatum* Horstmann, *rectificator* Aubert.

4. *Diadegma flexum* subgroup: Ovipositor sheaths 1.7–2.0 times as long as the first tergite of the gaster, ovipositor conspicuously upcurved near the tip (possible synapomorphy) (Figs 13, 14). Claws inconspicuously pectinate (as in Fig. 7), the subapical teeth less than half as long as the apical one. Hosts unknown. Species: *flexum* Horstmann, *pulicator* Aubert.

PRESENTATION OF RECORDS

All specimens (or parts of series) listed have been determined by KH. Hosts are given the names currently believed to be valid, with synonymy (as labelled) also given. Foodplants are cited only when they have appeared on the data label. While each individual rearing is regarded as a record, the summary we give also includes (in brackets) the number of independent collections listed—i.e. differing in either host, foodplant or place. Place name, country abbreviation, and depository (or depositories) for the specimens are given for each independent collection:

the numbers of specimens recorded against each host/foodplant category are divided according to depository so that each specimen remains traceable, but otherwise they are bulked together.

Abbreviations used are: [for countries] A = Austria; BG = Bulgaria; BY = Belarus; CH = Switzerland; D = Germany; DEN = Denmark; F = France; FIN = Finland; GB = Great Britain; GR = Greece; H = Hungary; I = Italy; IRL = Ireland; M = Moldavia; N = Norway; NL = Netherlands; P = Portugal; PL = Poland; R = Russia; S = Sweden; Y = former Yugoslavia, and [for depositories] Aeschlimann = private collection, Montpellier; Aubert = Aubert collection in Musée Zoologique, Lausanne; Bauer = private collection, Großschwarzenlohe/Nürnberg; Bridgman = Bridgman collection in Castle Museum, Norwich; Budapest = Természettudományi Múzeum Allattára; Eberswalde = Deutsches Entomologisches Institut; Haeselbarth = Haeselbarth collection in Zoologische Staatssammlung, München; Hilpert = Hilpert collection in Landessammlungen für Naturkunde, Karlsruhe; Hinz = Hinz collection in Zoologische Staatssammlung, München; Horstmann = private collection, Würzburg; Huemer = private collection, Innsbruck; Jordan = private collection, Soyhières/Delémont; Jussila = private collection, Turku; Kolarov = private collection, Sofia; Leiden = Nationaal Natuurhistorisch Museum; London = Natural History Museum; Lund = Zoologiska Institution; München = Zoologische Staatssammlung; NMS = National Museums of Scotland, Edinburgh (includes Shaw collection); Rill = Rill collection in Zoologisches Museum, Kiel; St. Petersburg = Zoological Institute, Academy of Sciences; Sawoniewicz = private collection, Warszawa; Šedivý = private collection, Praha; Stockholm = Naturhistoriska Riksmuseet; Strobl = Strobl collection in Benediktinerabtei, Admont; Torino = Museo Regionale di Scienze Naturali; Wrocław = Muzeum Przyrodnicze.

Knowledge of voltinism and phenology are important in understanding host range, and we have expressed this largely from material in NMS, most of which comes from GB. We use the term "bivoltine" to indicate at least two generations, though recognising that in practice more than one "summer" (= non-diapause) generation is likely to arise under favourable conditions in species that exhibit such a generation. It is also possible that some species will show more obligate differences in voltinism in different parts of their range. Campopleginae is not one of the subfamilies of Ichneumonidae known to include species that overwinter as adults in temperate climates and we presume that the only options open to the species we are dealing with are to overwinter as a cocooned stage or as a young larva in a host that overwinters partly grown. This is also consistent with the general view of Campopleginae as being pro-ovigenic and having a relatively short adult life. It is not certain for any of these parasitoids at what stage in its larval life the host is attacked, but it seems likely to happen relatively early in most or perhaps all cases. Many of the hosts involved change their mode of feeding part of the way through their larval life and, when relevant, attention is drawn to this in the commentary. Information on host biology has been directly observed or taken from Emmet (1988, 1991).

A table of the number of rearings included in this paper from each host genus is also given (Table 1). As the Lepidoptera in general have been extensively sampled, this indicates the tightness of the host groups involved overall. The table also records the *Diadegma* species reared from each host genus. This allows host utilization patterns to be overviewed, and it also reveals the cases in which more than one *Diadegma* species is associated with a host genus.

KEY

Specimens of the *Diadegma nanus* group are small or very small, and have very few distinctive characters. Males usually cannot be determined, and the determination of females is likely to be uncertain in many cases, especially if only one specimen is available for examination. The specimens must be very carefully mounted, with all parts of the body clearly visible (especially the pleurae, the propodeum and the gaster from above and from one side), and with the apical tergites of the gaster and the ovipositor in their normal positions. The latter is often not the case in material collected or preserved in liquid, and the determination of those specimens may be particularly difficult or impossible. The key to species given here was difficult to construct and may prove difficult to use unless reliably determined

material is also available for comparison. In particular this is necessary to guard against misidentifying specimens of additional (= undescribed) species, which may be fairly numerous. For this reason four segregates that probably represent undescribed species are included in the key (and their rearing data are listed after the other species).

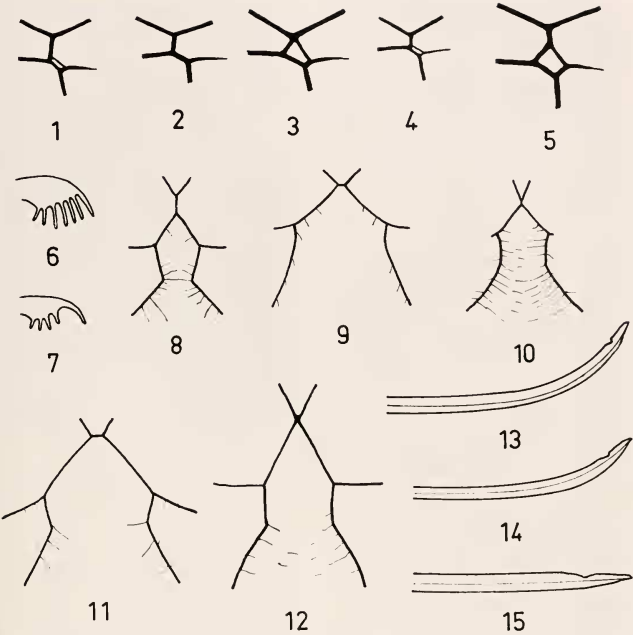
Among the most important characters are the colour of the hind tibiae and the ovipositor length. The colour of the hind tibiae refers to the outer aspect (the inner side is usually red or reddish brown) which is whitish or yellowish red basally and medially, and usually brownish or black subbasally and apically. The ovipositor length is expressed as an index, being the ratio of the visible length of the ovipositor sheaths (seen from the side) to the length of the first tergite of the gaster (measured along the dorsal surface).

KEY TO FEMALES OF THE *DIADEGMA NANUS* SPECIES GROUP IN WESTERN EUROPE

1. Ovipositor not or hardly surpassing tip of gaster, ovipositor index 0.3. (Areolet open (as in Fig. 2). Area superomedia 1.0–1.3 times as long as wide, constricted caudally and usually closed by a wrinkle (Fig. 8)) 2
 - Ovipositor surpassing tip of gaster, ovipositor index at least 0.4. (Other characters variable) 3
2. Scape ventrally, front and middle coxae whitish to whitish yellow. Hind femora for the greater part light red. Third tergite of the gaster to a varying extent yellowish red *crassum* (Bridgman)
 - Scape, front and middle coxae, hind femora and gaster usually totally dark brown or black. Sometimes tips of coxae and small lateral spots on third tergite of gaster yellowish *pusio* (Holmgren)
3. Hind femora dark brown or black and ovipositor index 0.5–0.8 (*D. crataegi* and *D. exareolator* with ovipositor index 0.9–1.0 sometimes have dark hind femora and may run here, but *D. crataegi* differs by the area superomedia 1.3–1.5 times as long as wide, and *D. exareolator* differs by the combination of an open areolet and the hind tibiae whitish basally and medially) 4
 - Hind femora yellowish red to reddish brown, sometimes darkened basally and apically, and/or ovipositor longer 9
4. Area superomedia 1.7 times as wide as long, extended caudally, grading into area petiolaris with almost no boundary (Fig. 9). Areolet very oblique, closed by a faint vein (Fig. 1). Second tergite of gaster as long as wide. (Ovipositor index 0.6) *scotiae* (Bridgman)
 - Area superomedia at most 1.3 times as wide as long, usually with parallel sides or somewhat constricted caudally (Fig. 10). Areolet open or closed. Second tergite of gaster at least 1.1 times as long as wide 5

5. Areolet closed by a faint vein. Area superomedia usually somewhat wider than long. Ovipositor index 0.5–0.7. (Hind tibiae whitish to whitish yellow medially)	6
– Areolet open (Fig. 2). Area superomedia as long as wide or somewhat longer than wide (Fig. 10). Ovipositor index 0.7–0.8	7
6. Postpetiole about 0.9 times as long as wide. Second tergite of gaster 1.0–1.1 times as long as wide. Scape and coxae dark brown or black	<i>laricinellum</i> (Strobl)
– Postpetiole about 1.1 times as long as wide. Second tergite of gaster 1.5 times as long as wide. Scape ventrally, front coxae and middle coxae apically conspicuously yellow	<i>tamariscator</i> (Aubert)
7. Hind tibiae whitish medially	species 1
– Hind tibiae yellowish brown medially	8
8. Mesopleura with fine and irregular wrinkles dorsally and medially. Postpectal carina incised centrally	<i>callisto</i> Horstmann
– Mesopleura coriaceous dorsally and medially. Postpectal carina straight or somewhat bent centrally	<i>elishae</i> (Bridgman)
9. Ovipositor index 0.4–0.6. (Flagellum filiform, scarcely wider medially than subapically. Hind tibiae whitish to whitish yellow basally and medially, yellowish brown to medium brown subbasally and apically)	10
– Ovipositor index at least 0.6 (<i>D. brevivalue</i> with an index of 0.6–0.7 has the flagellum fusiform and the hind tibiae yellowish red basally and medially and not darkened subbasally)	11
10. Ovipositor index 0.4. Front and middle coxae whitish yellow. Gaster to a varying extent reddish or reddish brown. Areolet closed by a very faint vein or open	<i>micrurum</i> (Thomson)
– Ovipositor index 0.5–0.6. Coxae and gaster black, at most tips of front coxae whitish yellow. Areolet open	<i>melanium</i> (Thomson)
11. Ovipositor index 0.6–0.7. Hind tibiae yellowish red, with only a narrow light brown ring apically. Flagellum fusiform, 1.3 times as wide medially as subapically. (Arolet closed)	<i>brevivalue</i> (Thomson)
– Ovipositor index at least 0.8. Hind tibiae usually darkened subbasally and apically, though sometimes inconspicuously. Flagellum often filiform	12
12. Ovipositor index 0.8–1.0 and hind tibiae yellowish to yellowish red basally and medially, yellowish brown to light brown subbasally and apically, with little contrast. Front and middle coxae for the greater part or totally whitish yellow	13
– Ovipositor index at least 1.2 and/or hind tibiae whitish to whitish yellow basally and medially, medium brown to black subbasally and apically, with much contrast. Front and middle coxae often black	14
13. Area petiolaris with fine but conspicuous transverse wrinkles. Areolet usually closed. Ovipositor index 0.8–0.9. Base of flagellum often somewhat yellowish brown ventrally	<i>anurum</i> (Thomson)
– Area petiolaris coriaceous. Areolet open. Ovipositor index 0.9–1.0. Base of flagellum dark brown	<i>lithocolletis</i> Horstmann
14. Ovipositor index 0.8–1.1. (Hind tibiae whitish to whitish yellow basally and medially, medium to dark brown or black subbasally and apically, with much contrast)	15
– Ovipositor index at least 1.1 (<i>D. ledicola</i> with an index of 1.1–1.2 has the hind tibiae with less contrast)	20
15. Areolet open. (Ovipositor index 0.9–1.0. Hind tibiae whitish basally and medially, brownish black to black subbasally and apically)	<i>exareolator</i> Aubert
– Areolet closed (except as an aberration)	16
16. Scape ventrally and front and middle coxae usually conspicuously whitish yellow, or middle coxae for the greater part black. (Area superomedia 0.9–1.1 times as long as wide. Ovipositor index 0.8–0.9. Hind tibiae whitish to whitish yellow basally and medially, brownish black to black subbasally and apically)	<i>stigmatellae</i> Horstmann

- Scape and coxae dark brown or black, at most tips of front coxae whitish 17
- 17. Hind tibiae medium brown subbasally, dark brown apically. Area superomedia 1.0–1.1 times as long as wide. (Ovipositor index 0.9–1.1) *holopygum* (Thomson)
- Hind tibiae brownish black to black subbasally as well as apically. Area superomedia 1.1–1.5 times as long as wide 18
- 18. Area superomedia 1.3–1.5 times as long as wide. Ovipositor index 0.9–1.0. Body length 3–4 mm *crataegi* Horstmann
- Area superomedia 1.1–1.2 times as long as wide. Ovipositor index 0.8–0.9. Body length 4–5 mm 19
- 19. Hind legs very slender, hind femora 5.4–5.7 times as long as wide species 2
- Hind femora 4.6–4.9 times as long as wide species 3
- 20. Claws conspicuously pectinate, the subapical teeth of hind claws nearly as long as the apical one (Fig. 6). Second tergite of gaster 0.8 times as long as wide. (Ovipositor index 1.4–1.6) *latungulum* (Thomson)
- Claws not so strongly pectinate, subapical teeth conspicuously shorter than the apical one (Fig. 7). Second tergite of gaster at least as long as wide 21
- 21. Ovipositor index 1.1–1.5 22
- Ovipositor index 1.7–2.0 27
- 22. Hind tibiae light red, with a yellow spot basally, scarcely darkened subbasally and apically. Third tergite of gaster for the greater part or totally light red. (Ovipositor index 1.3–1.4) *rufatum* (Bridgman)
- Hind tibiae with more contrast. Third tergite of gaster for the greater part or totally black 23
- 23. Hind tibiae yellowish to light red basally and medially, light to medium brown subbasally, medium to dark brown apically, with less contrast 24
- Hind tibiae whitish basally and medially, medium brown to black subbasally and apically, with much contrast 25
- 24. Second tergite of gaster 1.1–1.3 times as long as wide. Ovipositor index 1.1–1.2. Scape ventrally, front and middle coxae usually for the greater part or totally yellowish to light red *ledicola* Horstmann
- Second tergite of gaster 0.9–1.0 times as long as wide. Ovipositor index 1.2–1.5. Scape, front and middle coxae usually for the greater part or totally black *consumptor* (Gravenhorst)
- 25. Body length 2–3 mm. Hind tibiae dark brown to black subbasally. (Area petiolaris with conspicuous transverse wrinkles. Ovipositor index 1.2–1.3) *nanus* (Gravenhorst)
- Body length 4–5 mm. Hind tibiae medium brown subbasally 26
- 26. Area petiolaris with conspicuous transverse wrinkles. (Ovipositor index 1.2–1.5) *duplicatum* Horstmann
- Area petiolaris coriaceous, without transverse wrinkles. (Ovipositor index 1.2) ... species 4
- 27. Ovipositor conspicuously upcurved near tip (Figs 13, 14) 28
- Ovipositor straight over its total length (Fig. 15) 29
- 28. Body length 4–5 mm. Areolet large, touching radius (or nearly so) (Fig. 3). Ovipositor very conspicuously upcurved near tip (Fig. 13). (Ovipositor index 1.7–2.0) *flexum* Horstmann
- Body length 3.3 mm. Areolet very small, very oblique (Fig. 4). Ovipositor less conspicuously upcurved near tip (Fig. 14). (Ovipositor index 1.8) *pulicator* Aubert
- 29. Areolet oblique, with second recurrent vein distal to middle (Fig. 5). Area superomedia somewhat wider than long (Fig. 11). (Ovipositor index 1.7–2.0) *longicaudatum* Horstmann
- Areolet regular, with second recurrent vein in middle. Area superomedia 1.2 times as long as wide (Fig. 12). (Ovipositor index 1.7) *rectificator* Aubert



Figs. 1-5. Areolet of fore wing. Fig. 1: *Diadegma scotiae* (Bridgman); Fig. 2: *D. elishae* (Bridgman); Fig. 3: *D. flexum* Horstmann; Fig. 4: *D. pulicator* Aubert; Fig. 5: *D. longicaudatum* Horstmann. Figs 6-7. Claw of hind leg. Fig. 6: *D. latungulum* (Thomson); Fig. 7: *D. longicaudatum* Horstmann. Figs 8-12. Area superomedia of propodeum. Fig. 8: *D. pusio* (Holmgren); Fig. 9: *D. scotiae* (Bridgman); Fig. 10: *D. elishae* (Bridgman); Fig. 11: *D. longicaudatum* Horstmann; Fig. 12: *D. rectificator* Aubert. Figs 13-15. Ovipositor tip. Fig. 13: *D. flexum* Horstmann; Fig. 14: *D. pulicator* Aubert; Fig. 15: *D. longicaudatum* Horstmann.

REARING AND DISTRIBUTION
RECORDS, ANALYSES OF HOST
RANGE AND TAXONOMIC REMARKS

Diadegma anurum (Thomson)

Tischeria ekebladella (Bjerkander) (Tischeriidae)
on *Quercus robur*: 2 ♀ Methven Wood/
Perths./GB (NMS), 2 ♀ Wytham Wood/
Oxon/GB (Horstmann, NMS), 25 ♀ Kiel/D
(Horstmann, Jordan).

29 (3 independent) records: one host species. Univoltine in Britain, like its host which is a leaf miner throughout its pre-imaginal life. *D. anurum* overwinters in the host's pupation disc in the mine following leaf fall, in which it makes its own cocoon. Only females have been seen and it is probably thelytokous.

Distribution.—Reared: D, GB. Non-reared:

D (Haeselbarth, Hilpert, Horstmann), M (St. Petersburg), PL (Sawoniewicz), S (Lund).

Diadegma brevivalve (Thomson)

Epermenia illigerella (Hübner) (Epermeniidae): 2 ♀, 2 ♂ Eberswalde/D (Eberswalde, Horstmann), 1 ♀ Goslar/D (München).

5 (2 independent) records: one host species (feeding on Umbelliferae). Scholz (1996) has recently shown that two taxa have been confused under the host name *illigerella*, and it is possible that these records might be referable to *Epermenia falciformis* (Haworth). In Britain the *Epermenia* formerly referred to *E. illigerella* appear all to belong to *E. falciformis* (Godfray & Sterling 1996). This species is bivoltine, feeding on *Angelica* or *Aegopodium*, the first generation in spun leaflets and the second by mining a branch stem into the umbel, and the winter may be passed as an egg. It is not clear whether or how the life history of *E. illigerella* differs, or which of the possible host species occur in the areas where *D. brevivalve* has been found. *D. brevivalve* is probably a highly specialised parasitoid, but the available rearing data are insufficiently clear to suggest voltinism or how the winter is passed.

Distribution.—Reared: D. Non-reared: D (Horstmann), R (St Petersburg), S (Lund).

Diadegma callisto Horstmann

Callisto coffeella (Zetterstedt) (Gracillariidae) on *Salix silesiaca*: 3 ♀, 7 ♂ Tatry/PL (Horstmann, Sawoniewicz).

10 (1 independent) records: one host species. Apparently highly host specialised. The host at first feeds in a mine, and subsequently in a folded leaf. It is (in Britain) univoltine and overwinters in the cocoon stage. The available rearing data for *D. callisto* are not precise enough to be indicative of voltinism or the overwintering stage.

Distribution.—Reared: PL.

Diadegma consumptor (Gravenhorst)

No host record.

Aubert (1971: 38 f.) described a subspecies *alpestrator* Aubert from the Alps, which agrees with the lectotype of *D. consumptor* in structure, proportions and general colour pattern, but differs from it by its darker colour (scape, legs). However, very little is known about the distribution and variability of *D. consumptor*. The lectotype (from Genoa), which is both aged and damaged, is the only specimen so far attributed to the nominate subspecies, and at least one intermediate has been seen from within the distributional area of the supposed subspecies *alpestrator*. It is our view that recognition of two subspecies is unwarranted and *alpestrator* Aubert is here formally reunited with the nominate subspecies (*syn. nov.*).

Distribution.—Non-reared: A (Horstmann), CH (Lund), F (Aubert), I (Haeselbarth, Horstmann, Wrocław).

Diadegma crassum (Bridgman)

Ectoedemia argyropeza (Zeller) (Nepticulidae): 1 ♂ Innsbruck/A (München).

Bucculatrix bechsteinella (Bechstein & Scharfenberg) (*syn. crataegi* Zeller) (Bucculatricidae) on *Crataegus* sp.: 2 ♀ Pitt Down/Winchester/Hants./GB (NMS).

Bucculatrix cidarella Zeller on *Alnus glutinosa*: 1 ♀, 3 ♂ Bremen/D (Horstmann, München), 1 ♀ Puszca Borecka/Gizycko/PL (Sawoniewicz), 7 ♀, 5 ♂ Emer Bog/Hants./GB (Horstmann, NMS); on unrecorded plant: 1 ♂ Abbots Wood/Sussex/GB (Bridgman), 1 ♀ Trelasker/Cornwall/GB (NMS).

Bucculatrix demaryella (Duponchel) on *Betula pubescens*: 2 ♀ Soldany/Wegorzewo/PL (Sawoniewicz); on unrecorded plant: 6 ♀ Watlington/Kent/GB (NMS), 1 ♀ Horsham/Sussex/GB (Bridgman), 1 ♂ Hawks Wood/Cornwall/GB (NMS).

Bucculatrix frangutella (Goeze) (*syn. alnella* (Villers)) on *Frangula alnus*: 3 ♀ Wageningen/NL (NMS); on *Rhamnus catharticus*: 1 ♀ Chippenham Fen/Cambs./GB (NMS).

Bucculatrix thoracella (Thunberg) on *Tilia* sp.: 1 ♂ Bristol/GB (NMS).

Bucculatrix ulmella Zeller on *Quercus robur*: 4 ♀, 3 ♂ Botley Wood/Hants./GB (NMS).

Bucculatrix sp. on *Betula* sp.: 1 ♀ Hambergen/Osterholz-Scharmbeck/D, 1 ♀ Schierbrok/Delmenhorst/D (München).

Calybitis phasianipennella (Hübner) (Gracillariidae) on *Polygonum hydropiper*: 1 ♀ Oyter Moor/Bremen/D (München).

47 (18 independent) records: 45 (96%) are from *Bucculatrix* (6 species). While the other two should be regarded with considerable suspicion (the final instar larvae of *Bucculatrix* species are notorious for straying widely from their foodplant before constructing their cocoons, making their accidental inclusion in other samples particularly likely to happen), the fact that both of these supposed hosts start out as miners could also be taken to indicate some plasticity at the periphery of the host range. All but one (ex *B. thoracella*) of the British specimens seen have overwintered in the host cocoon and, from its core host range of *Bucculatrix* species, *D. crassum* appears to be a univoltine parasitoid restricted to arboreal hosts that overwinter in the cocoon stage. Of the *Bucculatrix* species listed, only *B. ulmella* is normally bivoltine in Britain. The host range of *D. crassum* contrasts with that of *D. pusio*, also a parasitoid of *Bucculatrix*, and the two species show colour differences (see key) that are consistent and without intermediates, even in series from the same locality and host (*B. ulmella* at Botley Wood and *B. demaryella* at Watlington; also *B. frangutella* at separate localities).

Distribution.—Reared: A, D, GB, NL, PL. Non-reared: D (Haeselbarth, Hilpert), PL (Sawoniewicz).

Diadegma crataegi Horstmann

Parornix anglicella (Stainton) (Gracillariidae) on *Crataegus monogyna*: 3 ♀ Medmenham/Bucks./GB, Wageningen/NL (NMS).

Parornix betulae (Stainton) on *Betula* sp.: 1 ♀ Ad-derstonelee Moss/Roxb./GB (NMS).

Parornix torquillella (Zeller) on *Prunus spinosa*: 1 ♀ Wester Frisk/Fife/GB (NMS).

Parornix sp. on *Prunus spinosa* or *Crataegus monogyna*: 1 ♀ Warton Crag/Lancs./GB (NMS).

Phyllonorycter blancardella (Fabricius) (Gracillariidae) on *Malus* sp.: 1 ♀ Doddyscombsleigh/Devon/GB (NMS).

Phyllonorycter corylifoliella (Hübner) on *Crataegus monogyna*: 1 ♀ Reading/Berks./GB (NMS).

Phyllonorycter oxyacanthae (Frey) on *Crataegus monogyna*: 4 ♀, 3 ♂ Lymm/Ches./GB (Horstmann, NMS, London), 1 ♀ Leigh Woods/Avon/GB (Horstmann).

Phyllonorycter sp. on *Quercus robur*: 1 ♀ Abbotts Moss/Ches./GB (NMS).

17 (10 independent) records: 7 host species, all in two genera of relatively small Gracillariidae mining trees and bushes (? especially *Rosaceae*) as young larvae. *Phyllonorycter* species continue to mine throughout their larval life and also pupate in the mine, while *Parornix* species make one or more leaf folds following a rather small *Phyllonorycter*-like mine, and finally pupate in a separate purpose-made site. Most (possibly all) of the rearings listed are from bivoltine hosts, and the rearing data suggest that their generations are attacked by successive generations of the parasitoid. All overwinter in the pupal stage: despite this, *D. crataegi* from these gracillariids collected in late summer or autumn seem always to have emerged as adults in autumn or early winter of the same year. This leaves its means of passing the winter unclear (presuming it cannot do so as an adult). Some aspect of the husbandry may have consistently led to unnaturally early emergence of the adults (i.e. instead of overwintering as a cocooned stage), or it is possible that there may be an overwintering generation in some other host that we have not yet found. Similar uncertainties arise for *D. duplicatum* and *D. stigmatellae*.

Distribution.—Reared: GB, NL.

Diadegma duplicatum Horstmann

Caloptilia stigmatella (Fabricius) (Gracillariidae) on *Populus tremula*: 2 ♀, 2 ♂ Hell Coppice/Bucks./GB, MonkWood/Worcs./GB, Loch

Fada/Isle of Coll/GB (NMS), 3 ♂ Waulkmill Bay/Orkney/GB (Horstmann, NMS); on *Salix alba*: 1 ♀ Bad Eilsen/Hameln/D (München); on *Salix aurita*: 1 ♀ Loch Fada/Isle of Coll/GB (NMS); on *Salix caprea*: 1 ♀ Broadmoor/Berks./GB (NMS); on *Salix cinerea* agg.: 5 ♀, 1 ♂ Oyter Moor/Bremen/D (Horstmann, München), 2 ♀ Southleigh/Devon/GB (Horstmann, NMS); on *Salix repens*: 1 ♀ Wedel/Hamburg/D (Haeselbarth), 3 ♀ Holme Chase/Devon/GB (NMS); on *Salix viminalis*: 1 ♀ Troisdorf/Köln/D (München), 1 ♀, 1 ♂ Woolhampton/Berks./GB (Horstmann, NMS); on *Salix* sp.: 1 ♀ Ettrick/Selkirk/GB (NMS); (cocoon collected on *Alnus glutinosa* growing near *Salix* sp.): 1 ♀ Caerlaverock Castle/Dumfries/GB (NMS); (labelled as from *Alnus* sp.): 5 ♀ Bremen/D (Horstmann, München).

Lyonetia pulverulentella Zeller (syn. *frigidariella* Herrich-Schäffer) (Lyonetiidae): 3 ♀ Edsäsens/Undersåker/Jämtland/S (Lund).

35 (17 independent) records: 32 (91%) from a single host species, that is predominantly univoltine in Britain and overwinters as an adult. *C. stigmatella* normally feeds on Salicaceae, though it has also occasionally been recorded on both *Betula* and *Alnus*. We accept the above host determinations of *C. stigmatella* from *Alnus* on the grounds that both the cocoon (in which the parasitoid's cocoon is formed) and the adult of *C. stigmatella* differ markedly from the common *Alnus*-feeding species, *Caloptilia elongella*. *Caloptilia* species are leaf miners when small, and it seems significant that the only host recorded above (3 individuals, but only one independent record) that is not *C. stigmatella* is, although in a different family, also a miner on Salicaceae: whether this resulted from a misidentification of possibly similar mines, as that of *C. stigmatella* is abnormally linear and not unlike a *Lyonetia* mine at first, or demonstrates a niche-specialised extending host range of an otherwise highly monophagous species is unclear. The available rearing data from *C. stigmatella* also leave the question of how *D. duplicatum* overwinters unanswered, as

all cocoons have emerged in the year they were made. Although it seems to be a univoltine parasitoid tied to a univoltine host, there is thus a possibility that we have not yet recognised the host or adults of the overwintering generation of what is really a bivoltine parasitoid (see also comments under *D. crataegi* and *D. stigmatellae*).

D. duplicatum differs from *D. holopygum* only in the length of the ovipositor (ovipositor index 0.9–1.1 in *holopygum*, 1.2–1.5 in *duplicatum*). But because their host ranges seem to be appreciably different, and because the ovipositor length does not vary (beyond the limits given above) within series from the same locality and host, they are treated as separate species. They cannot be regarded as seasonal forms of the same taxon, as both can be adult in early autumn.

Distribution.—Reared: D, GB, S. Non-reared: BG (Kolarov).

Diadegma elishae (Bridgman)

Parornix alpicola (Wocke) (Gracillariidae) on *Dryas octopetala*: 1 ♀ Lüner See/Vorarlberg/A (Huemer).

Parornix devoniella (Stainton) (syn. *avellana* (Stainton)) on *Corylus avellana*: 2 ♀, 1 ♂ Kiel/D (Horstmann).

Parornix scoticella (Stainton) on *Sorbus aria*: 1 ♀, 1 ♂ Hambleden/Bucks./GB (NMS); on *Sorbus aucuparia*: 1 ♀ Alderley Edge/Ches./GB (Horstmann), 1 ♀ Pitlochry/Perths./GB (NMS).

Parornix torquillella (Zeller) on *Prunus spinosa*: 2 ♀, 1 ♂ Capperleuch/Peebles./GB, Crackington/Cornwall/GB (NMS).

Parornix sp. on *Prunus spinosa*: 1 ♀, 2 ♂ West Wycombe/Bucks./GB (Horstmann, NMS); on *Prunus spinosa* or *Crataegus* sp.: 1 ♀ Faringdon/Oxon/GB (NMS).

Phyllonorycter nicellii (Stainton) (Gracillariidae) on *Corylus avellana*: 1 ♀ Kiel/D (Horstmann).

(The types, 2 ♀, 2 ♂ (Bridgman), were reared from "either *Ornix* [= *Parornix*] *scoticella* or *Nepticula aucuparia* [sic] [= *Stigmella nylandriella* (Tengström)]" from an unnamed British locality but, although subsequent rearing records (of both *D.*

elishae and bona fide parasitoids of *Nep-ticulidae* would very strongly suggest the former, we have not included these specimens in the analysis).

16 (10 independent) records: 15 (94%) from one genus (4 or more species). The remaining record is of a host that makes a mine which we know from direct personal experience is extremely easily confused with the fold of *Parornix devoniella* and, although *Phyllonorycter* is closely related to *Parornix*, it is hard to be confident that the host determination is correct. Thus *D. elishae* appears to be a specialist parasitoid of the genus *Parornix*, and it is of interest that while the great majority of *Parornix* species feed on trees and bushes, there is also a record of *D. elishae* from one of the few that feeds on low plants (*Dryas*), though it may be significant that in its habitat *Dryas* is often as tall as any co-occurring vegetation. The 9 GB specimens are all from Rosaceae, and appear to reflect at least a strong leaning towards hosts on that plant family in GB, if not in the rest of Europe. The winter is passed in the cocoon stage by both parasitoid and hosts. The rearing data suggest that *D. elishae* may be partly bivoltine, but clear evidence is lacking.

Distribution.—Reared: A, D, GB. Non-reared: A (Horstmann), PL (Sawoniewicz), R (St. Petersburg).

Diadegma exareolator Aubert

Bedellia somnulentella (Zeller) (Lyoniidae) on *Calystegia sepium*: 7 ♀, 3 ♂ Chartres/Eure-et-Loir/F (Horstmann, NMS); on *Calystegia soldanella*: 2 ♀, 2 ♂ Kennack Sands/Cornwall/GB (NMS); on *Convolvulus arvensis*: 1 ♀ Darbres/Ardèche/F (NMS), 1 ♀, 2 ♂ Budapest/H (Budapest); on *Calystegia* or *Convolvulus*: 4 ♀, 6 ♂ Gwithian/Cornwall/GB, Hayling Island/Hants./GB, Horton/Glower/GB, Tillingham/Essex/GB (NMS); on unrecorded plant: 2 ♀, 1 ♂ Malta (NMS).

Aspilapteryx tringipennella (Zeller) (Gracillariidae) on *Plantago lanceolata*: 1 ♀, 2 ♂ Aviemore/Inverness./GB (NMS), 2 ♀, 2 ♂ Tantallon/E. Lothian/GB (Horstmann,

NMS); on unrecorded plant: 1 ♀ Portland/Dorset/GB (NMS), 3 ♂ Burren/Co. Clare/IRL (London).

Tebenna micalis (Mann) (Choreutidae) on *Pulicaria dysenterica*: 1 ♀ Noss Mayo/Devon/GB (NMS).

Digitivalva pulicariae (Klimesch) (Yponomeutidae): 3 ♀, 3 ♂ Hale/Cornwall/GB (London).

Paraswammerdamia lutarea (Haworth) (Yponomeutidae): 2 ♀, 2 ♂ Munster/Lüneburg/D (London).

Plutella xylostella (Linnaeus) (Yponomeutidae) on *Brassica rapa*: 2 ♀, 2 ♂ Kiel/D (Hinz, Horstmann).

57 (17 independent) records: although 31 (54%) are from a single species (*Bedellia somnulentella*), the remaining records cover a further 3 families and include highly migratory hosts. Rearing data indicate that the parasitoid is bivoltine, and cocoons appear to produce adults always in the year they are formed. All the hosts recorded above except *Paraswammerdamia lutarea* feed on low vegetation and two (*Tebenna micalis*, *Plutella xylostella*) feed by windowing beneath a web rather than by mining, as far as is known even when very young. *D. exareolator* clearly has a strong association with *Bedellia somnulentella* but we regard it as a species with a well diversified host range. The available rearing data suggest that *Aspilapteryx tringipennella*, which mines through the winter, regularly provides the means for *D. exareolator* to get through in a growing host, and that *Paraswammerdamia lutarea* is another host usable by the overwintering generation.

Distribution.—Reared: D, F, GB, H, IRL, Malta. Non-reared: BG (Kolarov), F (Aubert), P (NMS).

Diadegma flexum Horstmann

No host record.

Distribution.—Non-reared: BG (Kolarov), D (Haeselbarth, Hinz, Horstmann), 1 (Bauer, Haeselbarth).

Diadegma holopygum (Thomson)

Tischeria marginata (Haworth) (Tischeriidae) on *Rubus plicatus*: 1 ♀ Czestochowa/PL (Sawo-

- niewicz); on *Rubus caesius*: 1 ♀ Włocławek/PL (Sawoniewicz).
- Bucculatrix artemisiella* Herrich-Schäffer (syn. *artemisiae* auctt.) (Bucculatricidae) on *Artemisia campestris*: 3 ♀, 1 ♂ Toruń/PL (Sawoniewicz).
- Bucculatrix gnaphaliella* (Treitschke) on *Helichrysum arenarium*: 1 ♀ Nienawiszcz/Poznań/PL (Sawoniewicz).
- Lyonetia clerkella* (Linnaeus) (Lyonetiidae) on *Malus domestica*: 1 ♀, 1 ♂ Edinburgh/GB (NMS); on *Prunus avium*: 1 ♀ Feldkirch/Vorarlberg/A (Huemer); on unrecorded plant: 1 ♀, 1 ♂ Asker/Oslo/N (Šedivý).
- Lyonetia pulverulentella* Zeller (syn. *frigidiella* Herrich-Schäffer) on *Salix pentandra*: 2 ♀, 1 ♂ Puszcza Borecka/Gizycko/PL, Rezerwat Spytkowo/Gizycko/PL (Sawoniewicz).
- Aspilapteryx tringipennella* (Zeller) (Gracillariidae) on *Plantago lanceolata*: 2 ♀, 2 ♂ Ascot/Berks./GB (NMS).
- Calybites auroguttella* (Stephens) (Gracillariidae) on *Hypericum perforatum*: 2 ♀ Ipsden/Oxon/GB (NMS), 2 ♀, 2 ♂ Farnham Royal/Surrey/GB (London).
- Calybites phasianipennella* (Hübner) on *Polygonum hydropiper*: 5 ♀, 1 ♂ Oyter Moor/Bremen/D (Horstmann, München), 1 ♀ Oldenbüttel/Bremen/D (München), 1 ♀, 1 ♂ Toruń/PL (Sawoniewicz); on *Polygonum mite*: 1 ♀, 2 ♂ Czystochleb/Toruń/PL, Gizycko/PL (Sawoniewicz); on *Rumex acetosa*: 9 ♀, 4 ♂ Ascot/Berks./GB (Horstmann, NMS), 2 ♀, 4 ♂ St. Jean du Gard/Gard/F (NMS); on *Rumex* sp.: 3 ♀, 2 ♂ Whitbarrow Moss/Cum./GB (NMS).
- Parornix finitimella* (Zeller) (Gracillariidae) on *Prunus cerasifera*: 1 ♀ Gizycko/PL (Sawoniewicz).
- Phyllonorycter maestingella* (Müller) (syn. *faginel-la* (Zeller)) (Gracillariidae) on *Fagus sylvatica*: 2 ♀ Köln/D (München).
- Phyllonorycter sylvella* (Haworth) on *Acer campestre*: 1 ♀ Poznań/PL (Sawoniewicz).
- Coleophora fuscocuprella* Herrich-Schäffer (Coleophoridae) on *Corylus avellana*: 1 ♀ Ruhede/Skovlund/DEN (NMS).
- Coleophora violacea* (Haworth) on *Betula* sp.: 1 ♀ Havant Thicket/Hants./GB (NMS).
- Mompha locupletella* (Denis & Schiffmüller) (Momphidae) on *Epilobium montanum*: 1 ♀ Kinkajmy/Bartoszyce/PL (Sawoniewicz), 2 ♀, 1 ♂ Sparkwell/Devon/GB (Horstmann, NMS); on *Epilobium obscurum*: 2 ♀ Emer Bog/Hants./GB (NMS); on *Epilobium* sp.: 2 ♀, 4 ♂ Ballyonneely/Galway/IRL (NMS), 1 ♀, 2 ♂ Puszcza Borecka/Gizycko/PL (Sawoniewicz).
- Millieria dolosalis* (Heydenreich) (syn. *dolosana* auctt.) (Choreutidae) on *Aristolochia clematitis*: 1 ♀, 1 ♂ St. Jean du Gard/Gard/F (NMS); on *Aristolochia pistolochia*: 9 ♀, 7 ♂ Darbres/Ardèche/F (Horstmann, NMS).

100 (32 independent) records: although 50 (50%) are from Gracillariidae, and especially *Calybites*, 4 genera in that family are involved and overall the records span 7 families of Lepidoptera (15 species). Although a few records are from hosts on trees and bushes, most are from hosts feeding in the field layer, and a particular association with that sector of the overall habitat probably accounts for the lack of records from *Caloptilia* (which feed entirely on trees and shrubs) among the records for Gracillariidae. Cocoons of *D. holopygum* resulting in late summer or autumn always seem to emerge the same year, but the available rearing data suggest that *Aspilapteryx tringipennella* and *Mompha locupletella*, both of which mine through the winter, provide the regular means for this bivoltine parasitoid to go through in a growing host. The possible role of *Coleophora fuscocuprella* and *C. violacea* in this respect is interesting: each is one of relatively few arboreal *Coleophora* species that attains full growth in the autumn but does not pupate until spring, and the single *D. holopygum* reared from *C. violacea* emerged in spring from a host case collected the previous autumn. The emergence date for the specimen from *C. fuscocuprella* is uncertain.

Distribution.—Reared: A, D, DEN, F, GB, IRL, N, PL. Non-reared: BG (Kolarov), I (Haeselerbarth), PL (Horstmann), R (St. Petersburg), S (Lund).

Diadegma larinellum (Strobl)

Coleophora larinella (Hübner) (Coleophoridae) on *Larix decidua*: 1 ♀, 2 ♂ Farnham Royal/

Surrey/GB (London): 1 ♂ Fortingall/Perths./GB (NMS), 1 ♀, 1 ♂ Schleswig/D (Horstmann), 1 ♀, 1 ♂ Admont/Steiermark/A (Strobl), 1 ♀ Zerneß/Engadin/CH (Horstmann), 2 ♀, 2 ♂ Trimmis/Graubünden/CH, Scheid/Graubünden/CH, 1 ♀ Val Aurina/Südtirol/I (Aeschlimann).

14 (8 independent) records: one host species. The host starts its larval life as a needle miner without a case. It hibernates partly grown and is univoltine. The parasitoid is presumably also univoltine and is carried through the winter in the partly grown host, emergence taking place from the host case in early/mid summer.

Distribution.—Reared: A, CH, D, GB, I. Non-reared: R (St. Petersburg).

Diadegma latungulum (Thomson)

Mompha conturbatella (Hübner) (Mompidae) on *Epilobium angustifolium*: 6 ♀, 5 ♂ Broughton Down/Hants./GB, Lullingstone/Kent/GB, Silverwells/Berwicks./GB (NMS); on unrecorded plant: 1 ♀ Tjörnarp/Kristianstad/S (Lund).

Mompha epilobiella (Denis & Schiffermüller) (syn. *fulvescens* (Haworth)) on *Epilobium hirsutum*: 36 ♀, 20 ♂ Bromley/Kent/GB, Catfield/Norf./GB, Chichester/Sussex/GB, Feckenham Wild Moor/Worcs./GB, Horning/Norf./GB, Horseheath/Cambs./GB, Leckford/Hants./GB, Northwood Hill/Kent/GB, Solihull/Warwicks./GB, The Flits/Herefords./GB, Darbres/Ardèche/F (NMS), 2 ♀, 1 ♂ Rezerwat Laz Piwnicki/Torun/PL (Sawoniewicz); on *Epilobium* sp.: 2 ♀ Goslar/D, Bad Eilsen/Hameln/D (München), 2 ♀, 2 ♂ Kiel/D (Horstmann, Rill), 1 ♂ Alpernton/Middlesex/GB (London).

Mompha langiella (Hübner) (syn. *epilobiella* (Roemer) nec (Denis & Schiffermüller)) on *Circaea lutetiana*: 2 ♀ Coombe Martin/Devon/GB (NMS).

Mompha locupletella (Denis & Schiffermüller) on *Epilobium alsinifolium*: 1 ♂ Whitebrook/Monmouths./GB (NMS); on *Epilobium montanum*: 1 ♀ Havant Thicket/Hants./GB (NMS); on *Epilobium tetragonum*: 3 ♀, 1 ♂ Cadsonbury/Cornwall/GB, Plymouth/Devon/GB (NMS), 1 ♂ Sparkwell/Devon/GB (Horstmann); on

unrecorded plant: 1 ♀, 3 ♂ Cornwall/GB, Marwellham Quay/Devon/GB (NMS).

Mompha nodicolella Fuchs on *Epilobium angustifolium*: 1 ♀ Camberwell/London/GB (NMS), 9 ♀, 1 ♂ East Ham/Essex/GB (Horstmann, NMS).

Mompha ochraceella (Curtis) on *Epilobium hirsutum*: 3 ♀, 1 ♂ Bromley/Kent/GB, Worcester/GB, Bulford/Wilts./GB (NMS).

Mompha propinquella (Stainton) on *Epilobium tetragonum*: 2 ♂ Colypool/Devon/GB, Plympton/Devon/GB (NMS); on *Epilobium* sp.: 3 ♀ Plympton/Devon/GB, Ryton/Warwicks./GB (NMS).

Mompha subbistrigella (Haworth) on *Epilobium montanum*: 1 ♀ Winchester/Hants./GB (NMS); on *Epilobium* sp.: 1 ♀, 2 ♂ Brotheridge/Worcs./GB (NMS).

Mompha sp. on *Epilobium montanum*: 1 ♀, 2 ♂ Mühlhausen/Thüringen/D (München).

118 (39 independent) records: all from *Mompha* (8 species). The distribution of rearing records from the above *Mompha* species is an approximate reflection of sampling effort, but it is noteworthy that two other well-sampled but rather small species, *M. raschkiella* mining *Epilobium angustifolium* and *M. miscella* mining *Helianthemum*, have consistently failed to produce *D. latungulum* in GB (Shaw unpublished). The *Mompha* species attacked by *D. latungulum* use their foodplants in a variety of ways ranging from tightly spinning shoots to mining leaves, and galling or boring in stems and seedpods. *D. latungulum* is bivoltine and its cocoons invariably emerge in the year of formation. Some of the host species overwinter as adults and others as partly fed larvae: while *D. latungulum* is often an abundant parasitoid of summer larvae of the former category, its presence at a site appears to depend on the co-occurrence of *Mompha* species that overwinter as partly grown larvae thereby providing the means for it to overwinter.

We have examined the male syntype of *Pectinella latungula* (Thomson) var. *deleta* Morley and it appears to belong to *D. la-*

tungulum, as Fitton (1976: 342) has already supposed.

Distribution.—Reared: D, GB, PL, S. Non-reared: BG (Kolarov), D (Bauer, Haeselbarth, Hinz, Horstmann), F (Lund), FIN (Jussila), GB (London), Y (Sawoniewicz).

Diadegma ledicola Horstmann

Diplodoma herminata (Geoffroy) (Psychidae): 1 ♀ Monk Wood/Worcs./GB (NMS).

Oreopsyche matthesi Bourgogne (Psychidae): 1 ♀, 1 ♂ Montalegre/Vila Real/P (Aubert).

Proutia betulina (Zeller) (Psychidae): 2 ♀, 2 ♂ Hatert/Nijmegen/NL (Horstmann, München), 1 ♀ Groesbeek/NL, 1 ♀ Bremen/D (München).

Psyche casta (Pallas): 4 ♀, 1 ♂ Orpington/Kent/GB, Avon Gorge/Bristol/GB, Painswick/Glos./GB, South Stack/Anglesey/GB (NMS).

Psychidae Gen. sp. on *Ledum palustre*: 1 ♀, 1 ♂ Heidmoor/Segeberg/D (Horstmann), 1 ♀ Salemer Moor/Lauenburg/Elbe/D (Hinz).

17 (11 independent) records: all from Psychidae (4 or more species). The parasitoids have emerged from the host cases in the summer in which they were collected: as the known hosts are essentially synchronous, univoltine and overwinter partly grown it is probable that the parasitoid is also univoltine and overwinters in the young host larva.

Distribution.—Reared: D, GB, NL, P. Non-reared: BG (Hinz), BY (St. Petersburg), D (Hinz), F (Aeschlimann), M (St. Petersburg), P (Aubert).

Diadegma lithocolletis Horstmann

Bucculatrix nigricomella Zeller (Bucculatricidae) on *Chrysanthemum leucanthemum*: 1 ♀ Dunajek/Olecko/PL (Sawoniewicz).

Acrocercops imperialella (Zeller) (Gracillariidae): 1 ♀ Wicken Fen/Cambs./GB (NMS).

Callisto denticulella (Thunberg) (Gracillariidae) on *Malus domestica*: 1 ♀, 2 ♂ Gizycko/PL (Sawoniewicz).

Phyllonorycter emberizaepenella (Bouché) (Gracillariidae) on *Lonicera periclymenum*: 5 ♀, 2 ♂ Balmaha/Stirlings./GB, Endrick Mouth/Dunbartons./GB, Kilmelford/Argyll/GB, Meth-

ven/Perths./GB (NMS), 2 ♂ Presmennan/E. Lothian/GB (Horstmann, NMS), 3 ♀ Bremen/D (Hinz, Horstmann); on *Lonicera tatarica*: 1 ♀ Torun/PL (Sawoniewicz); on *Lonicera xylosteum*: 1 ♂ Gizycko/PL (Sawoniewicz); on *Lonicera* sp.: 2 ♀, 4 ♂ Hulshorst/Gelder Land/NL (NMS), 3 ♀ Wollah/Bremen/D (München); on unrecorded plant: 2 ♂ Hamburg/D (Haeselbarth), 2 ♂ Österlöv/Kristianstad/S (Lund), 1 ♂ Rotenburg/Bremen/D (München), 1 ♀ Reher Kratt/Itzehoe/D (Horstmann).

Phyllonorycter ulmifoliella (Hübner) on *Betula* sp.: 1 ♀ Harpstedt/Delmenhorst/D (München).

Perittia herrichiella (Herrich-Schäffer) (Elachistidae) on *Lonicera xylosteum*: 2 ♀ Blankenburg/Thüringen/D (Torino), 1 ♀, 3 ♂ Czerwony Dwor/Olecko/PL, Leszczewek/Suwalki/PL, Ojców/Kraków/PL (Sawoniewicz), 2 ♀, 1 ♂ Villars-Colmars/Alpes de Haute Provence/F (NMS).

44 (23 independent) records: although 38 (86%) are from just two species of leaf miners on *Lonicera* (*Phyllonorycter emberizaepenella* and *Perittia herrichiella*) these two are in different families and the full host list spans 5 genera in 3 families, on a range of field layer plants as well as trees. *D. lithocolletis* overwinters as a cocooned stage (the numerous specimens from *Ph. emberizaepenella* have all done so, within the exceptionally tough overwintering cocoons of the host: indeed, this peculiarity of the host may be an important determinant of host range within the genus *Phyllonorycter*). It is unclear whether *D. lithocolletis* is univoltine or bivoltine in the northern part of its range, but the fairly rapid emergence of cocoons from *Pe. herrichiella* in the same summer that they were formed suggests bivoltinism in S. Europe. *D. lithocolletis* exhibits an interesting host range with an undeniably strong association with certain miners on *Lonicera*, but with evidence of both selection (*Phyllonorycter trifasciella* (Haworth), also mining *Lonicera*, is a common and well-sampled host that has not so far yielded this parasitoid) and a host family extension even there, and enough records out-

side that core to indicate considerable plasticity and recruitment of a broader host spectrum.

Distribution.—Reared: D, F, GB, NL, PL, S. Non-reared: I (München).

Diadegma longicaudatum Horstmann

Bijugis bombycella (Denis & Schiffermüller) var. *silvicolella* Sieder (Psychidae): 1 ♀ Hochobir/Kärnten/A (München).

Sterrhopterix fusca (Haworth) (syn. *hirsutella* (Hübner)) (Psychidae): 2 ♀, 1 ♂ Braunschweig/D (Horstmann, München).

4 (2 independent) records: all from Psychidae (2 species). The available rearing data do not clearly indicate how *D. longicaudatum* overwinters, but field collection dates of adults suggest that it may be bivoltine.

Originally, *D. longicaudatum* Horstmann was described (Horstmann 1969: 445) from specimens with a longer ovipositor (index 1.9–2.0), and *D. germanicum* Horstmann subsequently (Horstmann 1973: 145) from specimens with a shorter ovipositor (index 1.7–1.8). In other respects the two taxa are similar. Subsequently intermediate forms have been found, even in series from the same locality, and therefore the two taxa are here synonymized (syn. nov.). Aubert (1976: 205) synonymized *D. germanicum* with *D. rectificator* Aubert (were this to be correct, *D. longicaudatum* would be the valid name of the species). But the differences given by Horstmann (1973: 145; see key) remain constant in all the material so far studied and therefore *D. rectificator* is still treated as a species separate from *D. longicaudatum*.

Distribution.—Reared: A, D. Non-reared: A (Haeselbarth, Horstmann), BG (Kolárov), D (Bauer, Haeselbarth, Hinz, Horstmann), F (Aubert, Horstmann, Leiden), H (Horstmann), PL (Sawoniewicz), R (St. Petersburg).

Diadegma melanium (Thomson)

Bucculatrix noltei Petry (Bucculatricidae) on *Artemisia vulgaris*: 1 ♀, 7 ♂ Smykovo/Ostroda/PL, Torun/PL (Sawoniewicz).

8 (2 independent) records: one host species. *D. melanium* is a rarely encountered species but it seems probable that it is a regular parasitoid of *B. noltei* (note, however, that this host does not occur throughout the distribution of *D. melanium*). The host is univoltine, feeds in late summer and overwinters in its cocoon. With a single exception collected in June, adults of *D. melanium* have been collected and reared only in July, and it seems likely also to be univoltine.

Distribution.—Reared: PL. Non-reared: D (Haeselbarth, Horstmann, München), GB (Bridgman), S (Lund).

Diadegma micrurum (Thomson)

No host record.

Distribution.—Non-reared: Nord/F (Lund), R (St. Petersburg).

Diadegma nanus (Gravenhorst)

Coleophora juncicolella Stainton (Coleophoridae) on *Calluna vulgaris*: 3 ♀ Muir of Dinnet/Aberdeens./GB (Horstmann, NMS).

3 (1 independent) records: one host species. The host is univoltine and overwinters partly grown, no doubt carrying the parasitoid through. *C. juncicolella* is not rare but it is local to heathland and moorland habitats and rather seldom reared. It seems probable that *D. nanus* will be found to be a specialised and regular parasitoid of it, though to date *D. nanus* has been regarded as a rare species.

Distribution.—Reared: GB. Non-reared: D (Horstmann), S (Lund).

Diadegma pulicator Aubert

No host record.

Distribution.—Non-reared: Alpes de Haute Provence/F (Aubert).

Diadegma pusio (Holmgren)

Bucculatrix absinthii Gärtner (Bucculatricidae) on *Artemisia absinthium*: 1 ♀ Råplinge/Öland/S (NMS).

Bucculatrix capreella Krogerus on *Achillea millefolium*: 5 ♀, 1 ♂ Aviemore/Inverness./GB, Invercauld/Aberdeens./GB (NMS).

Bucculatrix cidarella Zeller: 1 ♀, 1 ♂ Bexley/Kent/GB (London), 1 ♀ locality unknown (Bridgman).

Bucculatrix demaryella (Duponchel) on *Castanea sativa*: 2 ♀, 1 ♂ Watlington/Kent/GB (NMS).

Bucculatrix frangutella (Goeze) on *Rhamnus catharticus*: 1 ♀ Leckford/Hants./GB (NMS).

Bucculatrix laciniatella Bernander on *Artemisia laciniata*: 2 ♀, 1 ♂ Möckelmosen/Öland/S (NMS).

Bucculatrix nigricomella Zeller on *Leucanthemum vulgare*: 1 ♀, 1 ♂ Blackford/Edinburgh/GB (Horstmann, NMS), 1 ♂ Whitstable/Kent/GB (NMS).

Bucculatrix noltei Petry on *Artemisia vulgaris*: 1 ♀ Torun/PL (Sawoniewicz); on unrecorded plant: 2 ♀, 2 ♂ Büchen/Lauenburg/Elbe/D (Horstmann, Rill).

Bucculatrix ulmella Zeller on *Quercus robur*: 3 ♀ Botley Wood/Hants./GB, Colchester/Essex/GB, Wimbledon Common/London/GB (NMS).

28 (15 independent) records: all from *Bucculatrix* (9 species). The rearing data indicate that *D. pusio* is a bivoltine taxon specialist, using as summer hosts *Bucculatrix* species that are univoltine or bivoltine on plants in the field layer but in either case that do not overwinter in the cocoon stage, and then for its overwintering generation attacking arboreal *Bucculatrix* species that do overwinter in the cocoon stage in the robust cocoons of which it also overwinters. (Contrast the host range of the apparently univoltine *D. crassum*, which has been reared only from the latter host group.)

Distribution.—Reared: D, GB, PL, S. Non-reared: A (Haeselbarth), GR (Lund), I (Haeselbarth), PL (Sawoniewicz), S (Stockholm).

Diadegma rectifactor Aubert

No host record.

Distribution.—Non-reared: P (Aubert).

Diadegma rufatum (Bridgman)

Prochoreutis myllerana (Fabricius) (Choreutidae) on *Scutellaria galericulata*: 4 ♀, 1 ♂ Oxford/GB (Horstmann, NMS), 2 ♂ Port Appin/Argyll/GB, Stover Park/Devon/GB (NMS); on *Scutellaria* sp.: 1 ♀ Bad Eilsen/Hameln/D (München); on unrecorded plant: 1 ♂ Woodbastwick/Norf./GB (NMS), 1 ♀ Kullen/Malmöhus/S (Lund).

Prochoreutis ?myllerana (as *Choreutes* [sic] *scintillulana* [sic]): 3 ♀, 3 ♂, unlocalised GB (Bridgman).

Prochoreutis sehestediana (Fabricius) on *Scutellaria galericulata*: 8 ♀, 8 ♂ Ashurst/Hants./GB, Barton Turf/Norf./GB, Catfield/Norf./GB (NMS); on *Scutellaria minor*: 1 ♀, 1 ♂ Plymouth/Devon/GB (NMS).

Prochoreutis myllerana or *P. sehestediana* on *Scutellaria galericulata*: 18 ♀, 12 ♂ Bexley/Kent/GB, Endrick Mouth/Stirlings./GB, Loch Tay/Perths./GB, Strumpshaw/Norf./GB (NMS).

64 (15 independent) records: all from the two species of *Prochoreutis* that occur in the region and feed on *Scutellaria*. *D. rufatum* is a highly specialised species and, like many parasitoids characteristic of wet habitats, is appreciably redder in colouration than most of its congeners. All of the many cocoons we have had alive have emerged in the year they were formed and, although the means by which *Prochoreutis* species (both of which are bivoltine) pass the winter is unclear, the rearing data suggest that *D. rufatum* is also a bivoltine species that overwinters in partly grown hosts.

Distribution.—Reared: D, GB, S. Non-reared: BY (St. Petersburg), D (Hilpert, Horstmann), PL (Sawoniewicz), S (Jussila, Lund).

Diadegma scotiae (Bridgman)

Phaulernis fulviguttella (Zeller) (Epermeniidae) on *Angelica sylvestris*: 1 ♀, 2 ♂ Glen Lyon/Perths./GB, Possil/Glasgow/GB (NMS), 3

♀, 2 ♂ Utsjoki/Kevo/FIN (Horstmann, Jusila); (as "*Heydenia auromaculella*") on unrecorded plant: 1 ♀, 5 ♂ Shetland/GB (Bridgman).

14 (4 independent) records: one host species. The host is univoltine, feeding in autumn among spun seeds and overwintering as a pupa. The two specimens of *D. scotiae* (from Glen Lyon) seen that are preserved with their cocoons emerged in August from the pupae (parasitoid cocoon spun within the host's pupal cuticle) of hosts collected as larvae the previous autumn. This use of host pupal cuticle is a regular practice of only a very small minority of Campoplegine, but it is seen in several genera. The specimens labelled as reared from "*Heydenia auromaculella*" are presumed to be from *P. fulviguttella* on the grounds that *Heydenia* Hofmann, 1868 (preocc.) was applied in Epermeniidae and the name *auromaculella* appears to be interpretable within British Epermeniidae only as a lapsus for *auromaculata* Frey, which is a synonym of *fulviguttella*. *D. scotiae* is a northern species and it is clear that it is univoltine.

Distribution.—Reared: FIN, GB. Non-reared: R (St. Petersburg).

Diadegma stigmatellae Horstmann

Caloptilia alchimiella (Scopoli) (Gracillariidae) on *Quercus robur*: 2 ♀ Innerleithen/Peebles./GB, Kerfield/Peebles./GB (NMS).

Caloptilia betulicola (Hering): 1 ♀ Chat Moss/Manchester/GB (NMS).

Caloptilia cuculipennella (Hübner) on *Ligustrum vulgare*: 8 ♀, 11 ♂ Branscombe/Devon/GB (Horstmann, NMS), 1 ♀, 1 ♂ Portland/Dorset/GB (NMS).

Caloptilia falcomipennella (Hübner) on *Alnus* sp.: 2 ♀ Bexley/Kent/GB, Medmenham/Bucks./GB (NMS).

Caloptilia robustella Jäckh on *Quercus robur*: 1 ♀ Reading/Berks./GB (NMS).

Caloptilia stigmatella (Fabricius) on *Populus alba*: 1 ♀, 2 ♂ Ainsdale/Lancs./GB (NMS); on *Populus nigra*: 1 ♀ Hampstead Heath/London/GB (NMS); on *Populus tremula*: 3 ♀ Milton Hide/Sussex/GB (NMS); on *Salix ci-*

neria agg.: 2 ♀, 4 ♂ Branscombe/Devon/GB, Southleigh/Devon/GB (NMS), 7 ♀, 5 ♂ Otmoor/Oxon/GB, Woodley/Berks./GB (Horstmann, NMS); on unrecorded plant: 2 ♀, 1 ♂ locality unknown (Bridgman); (labelled as from *Alnus* sp.): 3 ♀, 1 ♂ Bremen/D (Horstmann, München).

Caloptilia syringella (Fabricius): 2 ♀ Folkestone/Kent/GB (NMS).

Caloptilia sp. on *Quercus* sp.: 1 ♀ Coventry/Warwicks./GB (NMS).

Parornix anglicella (Stainton) (Gracillariidae) on *Crataegus monogyna*: 7 ♀, 4 ♂ Balgaverie/Ayrshire/GB, Bawsinch/Edinburgh/GB, Blackford Hill/Edinburgh/GB, Catfield/Norf./GB, Reading/Berks./GB, Spott/E. Lothian/GB (NMS).

Parornix finitimella (Zeller) on *Prunus spinosa*: 3 ♂ Noss Mayo/Devon/GB, Lower Earley/Berks./GB (NMS).

Parornix torquillella (Zeller) on *Prunus spinosa*: 20 ♀, 15 ♂ Balmaha/Stirlings./GB, Benane Head/Bute/GB, Blackford Hill/Edinburgh/GB, Chilbotton/Hants./GB, Clovenfords/Selkirs./GB, Endrick Mouth/Stirlings./GB, Morston/Norf./GB, Southleigh/Devon/GB, Tregroes/Cards./GB (NMS), 4 ♀, 6 ♂ Saffron Walden/Essex/GB (Horstmann, NMS).

Parornix sp. on *Prunus spinosa*: 4 ♀, 4 ♂ Hampstead Heath/London/GB, West Wycombe/Bucks./GB, Woodchester Park/Glos./GB (NMS).

129 (40 independent) records: all from two genera (10 species) of relatively large Gracillariidae that are at first leaf miners on trees and bushes and then fold leaves, finally pupating in a purpose-made site away from where they fed. We accept the record from *C. stigmatella* on *Alnus* on the grounds already outlined in the commentary for *Diadegma duplicatum*. The host group, broadly, has two generations in the summer both of which are attacked by *D. stigmatellae*, apparently successively. However, although some of the hosts (*Parornix* species, in particular) overwinter as pupae, cocooned stages of *D. stigmatellae* have appeared to be incapable of diapausing and adults have always emerged in the year cocoons are formed, even if emergence is late into the autumn or early win-

ter. Although we suspect that this may be a consequence of husbandry, we cannot discount the possibility that we may not have yet recognised the adults or hosts of the overwintering generation of this parasitoid, despite its being a widespread and abundant species in GB (see also remarks under *D. crataegi* and *D. duplicatum*).

Distribution.—Reared: D, GB. Non-reared: D (Horstmann), F (Leiden).

Diadegma tamariscator (Aubert)

No host record.

Distribution.—Non-reared: Corsica/F (Aubert). The specimen of uncertain status from Rhodes/GR (Lund) commented upon by Aubert (1989: 58) has also been examined, but its identity remains uncertain.

The following four series may each represent an undescribed species, but more material is needed to be certain of their status.

Diadegma species 1

Bucculatrix caprealla Krogerus (Bucculatricidae) on *Achillea millefolium*: 1 ♀ Granish Moor/Aviemore/Inverness./GB (NMS).

The host is univoltine and overwinters as an adult, but the parasitoid adult emerged in late July, soon after making its cocoon. This suggests that the parasitoid is not entirely specialised to this particular host.

Diadegma species 2

Caloptilia robustella Jäckh (Gracillariidae) on *Quercus robur*: 3 ♀, 1 ♂ Redgrave Fen/S.Lopham/Norfolk/GB (NMS).

The host is bivoltine and overwinters as a pupa. The parasitoids overwintered in their cocoons in the host cocoons and this taxon appears to be bivoltine. It is conceivable that it is specialised to this host.

Diadegma species 3

Elachista argentella (Clerck) (Elachistidae) on grasses: 2 ♀ Linkim Shore/Berwicks./GB (NMS).

The host is univoltine, and passes the winter as a partly fed larva. The rearing data suggest that the parasitoid is also univoltine, and that it overwinters as a larva in the host larva. It is conceivable that it is specialised to this host.

Diadegma species 4

Coleophora gryppipennella (Hübner) (Coleophoridae) on *Rosa* sp.: 2 ♀ Inverkeithing/Fife/GB (NMS).

The univoltine host overwinters as a partly fed larva, and the rearing data suggest that the parasitoid is similarly univoltine, overwintering as a larva inside its host. It is conceivable that it is specialised to this host.

DISCUSSION

The wide spectrum of host range characteristics revealed here for a group of closely related parasitoids warrants some discussion. There are, in fact, a number of threads that have a bearing on the complex processes in evolutionary ecology that must inevitably relate to speciation. To avoid the objection that the subgroups of the *D. nanus* group we have recognised are of uncertain relationship to one another, we will restrict comment to situations that pertain within the *D. nanus* subgroup, and clearly indicate the subgroup of any other species we mention.

It has been hypothesised (Shaw 1994) that in koinobiont parasitoids one way that new species first arise is as extreme specialists, and (for those that do not conserve and refine their extreme specialisation, as some certainly do) their host ranges may then tend to expand by a process of eventual (and incremental) recruitment of not only taxonomically related but also ecologically or physically similar hosts as they are encountered within a parasitoid's searching environment. This broadening of host range was regarded as providing the conditions that would promote the next speciation process, involving behav-

itorial specialisation on a fraction of that host range by a nascent species in response to sufficiently strong ecological opportunity and isolating mechanisms. General predictions of this hypothesis include the following. (1) While some parasitoids will be "taxon specialists" with host ranges that (at one extreme) may remain limited to a single species or (at the other extreme) may have broadened to involve many species in a given taxonomic group, there will also be parasitoids with host ranges that have broadened from some level of taxon specialisation so as also to encompass "ecologically" (including behaviourally or morphologically) similar but taxonomically unrelated hosts. (2) If it is particularly from species with broadened host ranges (whether remaining taxon specialists or not) that there is a tendency for nascent species to diverge through extreme specialisation in response to changing ecological opportunities, initially monophagous "young" species should arise that are most closely related to "old" species having wider host ranges. (3) Depending on the extent to which any subsequent tendency for the host ranges of the "young" species has had time and opportunity to occur (but presuming that it has been less manifest than in the "old" species), an overall pattern of very varied breadth of host range in closely related species would be expected, with no particular leaning towards close relationships between those having the narrowest (or the broadest) host ranges, but rather a tendency for species with broad host ranges to be most closely related to ("young") extreme specialists, with perhaps adjacent or shared hosts.

Unfortunately there are considerable difficulties in testing this hypothesis with appropriate rigour, as it would demand not only a very robust (and complete) phylogenetic reconstruction of the group of parasitoids in question, but also a clear knowledge of the host ranges and ecological circumstances pertaining at the time

the hypothesised speciation events took place. In more practical terms, there are probably insurmountable problems in trying to recognise and assign polarity to phylogenetically informative morphological character states separating genuine sister species that are so close and have diverged so recently that their current ecological attributes remain informative about conditions surrounding their divergence. Whether molecular techniques would offer better prospects is untested. At any rate, unfortunately we can be certain that currently we are not in a position to reconstruct the phylogeny of this group of *Diadegma* with any confidence: not only is there no definitive demonstration of monophyly in our interpretation of the *D. nanus* group, or even of any of its subgroups, but also the morphological features by which the species can be separated are very slight and reflect character states that are almost certainly highly labile and unpolarisable. On top of this there is little doubt that we know only a proportion of the extant species (quite apart from the prospect of there being extinct sister species), and we lack host range data for several of those that we do know. Nevertheless, the hypothesis connecting host range and speciation in koinobionts provides a framework against which to examine the pattern of host ranges seen in this group of *Diadegma* species, and if we are able to suggest close relationships between some species pairs it may inform, if not strictly test, the hypothesis.

There are seven described species (*anurum*, *brevivalve*, *callisto*, *laricinellum*, *melanium*, *nanus*, *scotiae*) known from only a single host species, five of them having been reared on more than one independent occasion. Another (*duplicatum*) probably falls into this category, allowing for the strong possibility that the singly independent anomalous host records may be the result of host misidentification. These may be absolute specialists: generally, most con-

genera and/or related genera of the known host have been sufficiently well sampled for us to be confident that the parasitoid certainly does not occur widely on them. Nine species (*crassum*, *crataegi*, *elishae*, *pusio*, *rufatum*, *stigmatellae*; *latungulum* of the *latungulum* subgroup; *ledicola* and *longicaudatum* of the *consumptor* subgroup) are also taxon specialists, albeit (to a variable extent) with wider host ranges: no recruitment of hosts seems to have occurred beyond a narrow range of taxonomically related hosts. In another three species (*exareolator*, *holopygum*, *lithocolletis*), however, host ranges are taxonomically much broader, and include hosts from several families—though not all hosts in those families are used. In these cases the host range has clearer ecological and possibly physical parameters than taxonomic ones, and it is suggested that these are the species which have incrementally broadened their host range by recruitment from disparate taxonomic groups, perhaps over long timescales but certainly from an initially narrow base.

In practice some of the absolute specialists may not be clearly differentiated as a category from the slightly more broadly based taxon specialists, if the host of the former kind has few close relatives within the parasitoid's searching environment available to be recruited. It may be significant, however, that the taxonomically most isolated species seem to be either absolute specialists (*brevivalve*, *scotiae*) or taxon specialists (*rufatum*, *latungulum* of the *latungulum* subgroup), as this might imply that these species, that have failed to appreciably broaden their host ranges, are "old specialists" which have not given rise to recognisable sister species in the relatively recent past. The trend seen here is consistent with the speciation hypothesis outlined by Shaw (1994), and it is also seen in *Aleiodes*. Moreover, as relatively isolated taxa within defined groups are easier to recognise than genuine sister species, examining other koinobiont groups

to see whether the most isolated species tend to be relatively taxon-specialised may provide the clearest test of the generality of this hypothesised link between host range expansion and subsequent speciation: if there is little evident trend it may suggest that this speciation mechanism is at best of minor importance in comparison with others. It is important, though, to apply the test the right way round—not to test whether taxon specialists tend to be abnormally isolated, as the hypothesised "young specialists" are expected not to be. One study that lends some support to this hypothesis is Gauld & Janzen's (1994) phylogenetic analysis of Costa Rican species of the campoplegine genus *Cryptophion*. Although they envisaged somewhat different evolutionary scenarios, they concluded that the most basal (i.e. the most isolated) species are taxon specialists, and that host range expansion has been an important force in the evolutionary biology of the group.

Some of the other specialists in our study (*anurum*, *callisto*, *duplicatum*, *laricinnellum*, *melanium*, *nanus*) belong to a central core of very closely related species that include those with the widest host range (*exareolator*, *holopygum*, *lithocolletis*) and, although sister species relationships cannot be suggested with confidence, this is also compatible with the speciation hypothesis, in which "young specialists" arise through speciation following host range diversification. Some putative pairs of "young specialists"/parent species from within this core group that would fit the hypothesis rather well are *anurum*/*lithocolletis* (possible synapomorphies: areolation of propodeum, colour of legs, ovipositor length, body size), *duplicatum*/*holopygum* (practically indistinguishable in all characters except length of ovipositor—see species entry for *D. duplicatum*) and *callisto*/*elishae* (practically indistinguishable in all characters except minor details of thorax—see key), but as already explained we are unable to claim that the

species tentatively paired are really the most closely related on objectively formulated grounds.

There are also some simpler influences on host range that can be clearly seen. In temperate climates the overwintering strategy of parasitoids is a key feature of their biology and the need to get through the winter often has a strong and evident bearing on host associations. In *Diadegma* species the two options for overwintering appear to be as a cocooned stage or as an early instar larva in a partially fed overwintering host larva. Collectively the host group of the species treated in this paper includes host species that overwinter in these two stages, but also hosts that overwinter in stages (egg, adult) in which these particular parasitoids are not carried.

In so far as they have been reared, the *Diadegma* species dealt with in this paper all kill the host as a prepupa (or pupa in the case of *scotiae*) and pupate within the host's pupation site. Their dependence on their hosts for pupation site selection (and the extent of host cocoon construction) is reflected by the overwintering strategy of the parasitoids: the only ones that definitely overwinter in the cocoon stage parasitise hosts that also overwinter in that stage in toughly constructed and/or cryptic sites (if *duplicatum* normally overwinters in the cocoon it represents an exception to this generalisation, though the cocoon of its host *Caloptilia* species, which overwinters as an adult, is as tough as those of the few *Caloptilia* species that overwinter in cocoons). This appears to reflect the need for a safe haven for this overwintering strategy, as the species that attack univoltine hosts which overwinter as eggs or adults are generally bivoltine species that overwinter in association with a different set of hosts, either in a protected cocoon (e.g. *pusio*) or as a young larva (e.g. *exareolator*, *holopygum*). From the viewpoint of the hosts, overwintering as non-susceptible stages and pupating

ephemerally in relatively exposed situations might be interpreted as a defensive strategy, as specialisation on such hosts is clearly difficult for parasitoids having the biology of *Diadegma*.

The hosts of the overwintering generation assume a high importance in the realised host range of some species (e.g. *exareolator*, *holopygum*; and *latungulum* of the *latungulum* subgroup), and these hosts may in fact be the more fundamental in the evolutionary ecology of the parasitoids, implying that host range expansion into summer hosts may have been a secondary process from an initially narrower univoltine base. Some of the data seem to be compatible with this: for example, there is what appears to be a closely related pair of species (*pusio* and *crassum*, which are practically indistinguishable except for colour: possible synapomorphies in areolation of propodeum, wing venation, ovipositor length) that attack essentially the same range of hosts in the overwintering generation, but only one is bivoltine and has summer hosts. While a fission into bivoltine and univoltine populations may have promoted a speciation, this has not resulted in a full separation of host range, perhaps because the summer hosts did not by themselves provide a possible route to speciation. If this speculation is correct in relation to the *pusio* (bivoltine)/*crassum* (univoltine) pair, it may be that a nascent species (*pusio*) has arisen as a direct result of a broadening of host range, not in this case by budding off as an extreme specialist. However, it is also possible that an ancestral bivoltine "old taxon specialist" (i.e. having recruited a wide range of *Bucculatrix* species as hosts) provided a base from which a univoltine species (*crassum*) budded off, with a suite of univoltine overwintering hosts already in place (conceivably promoted by a temporary or spatial scarcity of the summer hosts).

A difference in phenology resulting from changes in host range that restricts gene flow could often be important in the

speciation processes affecting temperate koinobionts, but the suggested mechanisms through which *pusio* and *crassum* might have separated, from "old taxon specialist" ancestry, appear not to be the most usual. It may be more significant that the putative "young specialist"/parent species pairs already discussed (*anurum/lithocolletis*, *duplicatum/holopygum* and *calisto/elishae*) involve apparently univoltine specialists and bivoltine parent species with a diversified host range; a pattern that is also discernible in the genus *Aleiodes* (Shaw 1994 and unpublished), in which there is some experimental evidence that a phenological difference of this kind may indeed be driving an incipient speciation.

Given the importance of understanding how the winter is passed it is unsatisfactory that for some species for which we have otherwise strong host range information (*crataegi*, *duplicatum*, *stigmatellae*) we cannot rule out the possibility that there is an overwintering generation on a completely different host group that we have not yet discovered. The latter three species all attack Gracillariidae and it is perhaps more likely that the methods used to rear the captive hosts (which either cannot or do not easily change their feeding site) in deteriorating autumn tree leaves is what has led to an abnormal emergence of the adults in the late autumn and early winter instead of the cocooned stage overwintering, in which case there would be no "missing" generation. More investigation is needed to settle this point, and also the remote possibility that these *Diadegma* species overwinter in the adult stage, but for now it seems parsimonious to suppose that the anomaly is just an artefact.

Host size is another factor that will almost certainly influence host range, though this influence is not necessarily easy to evaluate. There are four species (*crataegi*, *elishae*, *lithocolletis*, *stigmatellae*) that regularly use what appears to be a

largely non-overlapping range of arboreal Gracillariidae (i.e. not counting the specialists *calisto* and *duplicatum*). Notwithstanding the complication that these gracillariids have very differently structured parasitoid complexes as a consequence of host feeding biology (Askew & Shaw 1986), the four *Diadegma* species appear each to use quite discrete size ranges of host (*Parornix* and *Callisto* being on the whole intermediate in size between the larger *Caloptilia* and the smaller *Phyllonorycter*), and it is possible that the apparent partitioning within the overall host resource is essentially a matter of the parasitoids' being able to use hosts of only a particular, and rather narrow, size range. Against this, however, is the wide size range of the hosts of *D. exareolator*. The failure of *D. latungulum* (*D. latungulum* subgroup) to use the smallest *Epilobium*-feeding *Mompha*, *M. raschkiella*, in Britain may be for reasons other than its size, as the parasitoid complex of *M. raschkiella* is surprisingly different from that of its congeners in several other respects (Shaw unpublished).

The *D. nanus* subgroup has a very clear association with hosts that mine (at least in their early instars). This is perhaps most clearly seen from the usage of host families such as Epermeniidae and Choreutiidae (Table 1), in which several common and well-sampled species that do not have mining larvae are not attacked. These include the epermeniid *Epermenia chaerophyllella* (Goeze) (cf. Shaw & Aeschlimann 1994), and the choreutids *Choreutis pariana* (Clerck) (cf. Shaw 1984) and *Anthophila fabriciana* (Linnaeus) (Shaw unpublished). An interesting question arises from the probably complete failure (presuming the single record is erroneous) of the *D. nanus* group to have colonised potential host groups such as Nepticulidae. The generally small size of Nepticulidae (which is not only an extensive group of leaf miners but also a very thoroughly sampled one, cf. Askew & Shaw 1986, Askew 1994) does

Table 1. Overall host range of the *Diadegma nanus* group, given as the total number of records for each host genus recorded (with family totals in brackets). The parasitoid species concerned are listed in descending order in which they contribute to the number of records for the particular host genus.

Host genus	Number of records	<i>Diadegma</i> species
Nepticulidae (1)		
<i>Ectoedemia</i>	1	<i>crassum</i>
Tischeriidae (31)		
<i>Tischeria</i>	31	<i>anurum</i> , <i>holopygum</i>
Psychidae (21)		
<i>Bijugis</i>	1	<i>longicaudatum</i>
<i>Diplodoma</i>	1	<i>ledicola</i>
<i>Oreopsyche</i>	2	<i>ledicola</i>
<i>Proutia</i>	6	<i>ledicola</i>
<i>Psyche</i>	5	<i>ledicola</i>
<i>Sterrhopterix</i>	3	<i>longicaudatum</i>
Genus indet.	3	<i>ledicola</i>
Lyonetiidae (42)		
<i>Bedellia</i>	31	<i>exareolator</i>
<i>Lyonetia</i>	11	<i>holopygum</i> , <i>uplicatum</i>
Bucculatricidae (88)		
<i>Bucculatrix</i>	88	<i>crassum</i> , <i>pusio</i> , <i>melan-</i> <i>ium</i> , <i>holopygum</i> , <i>litho-</i> <i>colletis</i> , species 1
Gracillariidae (304)		
<i>Acrocercops</i>	1	<i>lithocolletis</i>
<i>Aspilapteryx</i>	15	<i>exareolator</i> , <i>holopygum</i>
<i>Callisto</i>	13	<i>callisto</i> , <i>lithocolletis</i>
<i>Caloptilia</i>	98	<i>stigmatellae</i> , <i>uplicatum</i> , species 2
<i>Calybites</i>	43	<i>holopygum</i> , <i>crassum</i>
<i>Parornix</i>	89	<i>stigmatellae</i> , <i>elishae</i> , <i>cra-</i> <i>taegi</i> , <i>holopygum</i>
<i>Phyllonorycter</i>	45	<i>lithocolletis</i> , <i>crataegi</i> , <i>hol-</i> <i>opygum</i> , <i>elishae</i>
Choreutidae (83)		
<i>Millieria</i>	18	<i>holopygum</i>
<i>Prochoreutis</i>	64	<i>rufatum</i>
<i>Tebenna</i>	1	<i>exareolator</i>
Yponomeutidae (14)		
<i>Paraswammerdamia</i>	4	<i>exareolator</i>
<i>Plutella</i>	4	<i>exareolator</i>
<i>Digitivalva</i>	6	<i>exareolator</i>
Epermeniidae (19)		
<i>Epermenia</i>	5	<i>brevivalve</i>
<i>Phaulernis</i>	14	<i>scotiae</i>

Table 1. Continued.

Host genus	Number of records	<i>Diadegma</i> species
Coleophoridae (21)		
<i>Coleophora</i>	21	<i>laricinellum</i> , <i>nanus</i> , <i>holo-</i> <i>pygum</i> , species 4
Elachistidae (11)		
<i>Perittia</i>	9	<i>lithocolletis</i>
<i>Elachista</i>	2	species 3
Momphidae (133)		
<i>Mompha</i>	133	<i>latungulum</i> , <i>holopygum</i>

not seem to be the answer, as there are several comparably small species of host (in the genera *Bucculatrix* and *Lyonetia* in particular) that are used by a number of these *Diadegma* species. The monotrysian family Nepticulidae is, however, a very in-pentetrable host group: the only ichneumonoid koinobionts that seem able to exploit it are the several subfamilies of Braconidae that are essentially specialists on that host group (cf. Shaw & Huddleston 1991), but it is not known whether the failure of others to do so is for reasons of competitive exclusion or physiological incompatibility. Dacnonypha (Eriocraniidae) and the monotrysian families Incurvariidae and Heliozelidae, that have been well sampled in the area, also seem free of attack, and it would be hard to interpret the failure to colonise these leaf mining hosts as a result of competitive displacement by more specialised ichneumonoids. It is worth noting, however, that there are some monotrysian hosts of the *D. nanus* group (Tischeriidae), though otherwise hosts are in the Ditrysia. The main under-represented lower ditrysian groups would appear to be Coleophoridae and Elachistidae, both of which have been well sampled and are known to suffer heavy parasitism from other parasitoid groups.

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